Prominent shoots are preferred: microhabitat preferences of *Maculinea alcon* ([Denis & Schiffermüller], 1775) in Northern Germany (Lycaenidae)

Annabell Küer[1] & Thomas Fartmann[2]

[1] Steinfurter Str. 502, D-48159 Münster, email: annabell.kueer@web.de
[2] Institute of Landscape Ecology, Department of Community Ecology, University of Münster, Robert-Koch-Straße 26, D-48149 Münster, email: fartmann@uni-muenster.de (corresponding author)

Abstract. The egg deposition behaviour of the Alcon Blue, *Maculinea alcon* ([Denis & Schiffermüller], 1775), was investigated in summer 2002 on a military training area near Osnabrück (North Rhine-Westphalia, Northern Germany). The study aims to analyse oviposition patterns on the flowers of the host plant *Gentiana pneumonanthe* (Marsh Gentian) and microhabitat characteristics of the chosen shoots. All possible host plants and all eggshells of *M. alcon* were counted and various characteristics of the host plant as well as the surrounding vegetation structure were recorded. A total of 1,787 eggs was counted on 124 out of 219 *Gentiana* shoots in an area of 3,200 m^2. About 70% were laid on the calyx and 25% on the flower. The vegetation (*Juncus-Succisa pratensis* association with patches of *Ericion tetralicis*) was generally dense and rather high. Occupied specimens had almost always a luxuriant growth and were mostly higher than the surrounding vegetation. In a logistic regression model the height-difference between the plant and the vegetation (prominence), the number of flowers per shoot, and the number of further shoots in the surrounding explained 78% of observed plant occupancy patterns. Finally suggestions to maintain and stabilize Alcon Blue populations are given.

Zusammenfassung. Das Eiablageverhalten des Lungenenzian-Ameisenbläulings, *Maculinea alcon* ([Denis & Schiffermüller], 1775), wurde im Sommer 2002 auf einem Truppenübungsplatz in der Nähe von Osnabrück (Nordrhein-Westfalen, Norddeutschland) untersucht. Ziel der Arbeit war es, Eiablagemuster an den Blüten der Wirtspflanze *Gentiana pneumonanthe* (Lungenenzian) sowie Mikrohabitatpräferenzen bei der Belegung zu studieren. Dazu wurden alle Lungenenziansprosse und die Eier von *M. alcon* gezählt. Verschiedene Parameter der Wirtspflanzen sowie die Vegetationsstruktur im Umkreis von 50 cm wurden aufgenommen. Von insgesamt 219 Sprossen auf einer Fläche von 3.200 m^2 waren 125 mit 1.787 Eiern belegt. Etwa 70% davon wurden an den Kelch geheftet und 25% an die Blüte. Die Vegetation (*Juncus-Succisa pratensis*-Assoziation mit einzelnen *Ericion tetralicis*-Flecken) war meist sehr dicht und relativ hoch. Belegte Lungenenzian-Exemplare waren in der Regel üppig und überragten größtenteils die umgebende Vegetation. Ein Modell der logistischen Regression zeigt, dass mit Hilfe der Höhendifferenz zwischen Spross und Vegetation, der Zahl der Blüten und der Anzahl der umgebenden Lungenenzian-Sprosse 78% der Daten korrekt vorhergesagt werden. Abschließend werden Vorschläge zum Erhalt und zur Stabilisierung von Populationen des Lungenenzian-Ameisenbläulings gemacht.

Key words. Alcon Blue, egg deposition, *Gentiana pneumonanthe*, *Maculinea alcon*, Marsh Gentian, management, microhabitat preferences, Germany.

Introduction

Habitat quality has been shown to be as important for the persistence of butterfly metapopulations as the degree of patch isolation and patch size (Anthes et al. 2003; Dennis & Eales 1997; Thomas et al. 2001). Thomas et al. (2001) and WallisDeVries (2004) pointed out that the criteria are not alternatives but should be considered complementarily. While many studies have recently addressed the effect of patch size and isolation on population dynamics for various butterflies, habitat quality is still comparably ill-defined for many endangered species. Habitat preferences of butterflies are often largely determined by the requirements of the preimaginal stages since the eggs are not and the larvae are only slightly mobile (Fartmann 2004; Porter 1992). In case of adverse weather or restricted food supply they are not able to escape. Therefore, the evaluation of habitat quality for a particular species requires a detailed knowledge of the preferences of ovipositing females and the survival of preimaginal stages under various conditions and across regions.

Here we studied the larval habitat preference of the Alcon Blue (*Maculinea alcon* ([Denis & Schiffermüller], 1775)). Although the butterfly genus *Maculinea* van Eecke, 1915 has attracted considerable attention because of its extraordinary relationship with ants of the genus *Myrmica* Latreille, 1804 (Munguira & Martin 1999; Als et al. 2004), recent descriptions of larval habitat requirements are scarce. The status of the Alcon Blue has been assessed as vulnerable in Europe (van Swaay & Warren 1999) and as endangered in Germany (Pretscher 1998); in North Rhine-Westphalia the species is critically endangered (Dudler et al. 1999). In many parts of Germany it is extinct (Fig. 1). Whereas quite a lot of research has addressed the relationship between *M. alcon* larvae and their host ants (e.g. Als et al. 2001; Elfferich 1988; Elmes et al. 1994; Liebig 1989; van Dyck et al. 2000), the relationship between *M. alcon* and its host plant *Gentiana pneumonanthe* (Marsh Gentian) is much less studied. Krismann (2000) studied oviposition patterns on the host plant and found a preference for egg-laying on the calyx. WallisDeVries (2004) compared habitat characteristics of occupied and unoccupied sites at a mesoscale of 10 × 10 m. The preferred vegetation structure for egg deposition is mostly known for the sibling species *Maculinea rebeli* (Hirschke, 1904) (Dolek et al. 1998; Kockelke et al. 1994; Meyer-Hozak 2000) but not for *M. alcon*, yet Marktanner (1985) observed that it avoids dense and overshadowed vegetation. The status of both forms as distinct species is strongly questioned by the recent genetical data (Als et al. 2004).

This study aims to increase our knowledge of the microhabitat structure at *M. alcon* oviposition sites. In particular we considered the following questions:

(i) What are the oviposition patterns on the Marsh Gentian?

(ii) Which kind of vegetation structure does the Alcon Blue prefer for egg deposition?

(iii) Which conclusions can be drawn for the management of the Alcon Blue sites?

Material and Methods

Study species. *Maculinea alcon* ([Denis & Schiffermüller], 1775) has a scattered distribution across Europe up to East Asia (Wynhoff 1998). In Germany the Alcon Blue is mainly found on the foothills of the Alps and in the Northwestern Lowlands (Fig. 1). Its flight period in Germany extends from early July to mid-August (Ebert & Rennwald 1991; Wynhoff et al. 1999). *M. alcon* thrives on moist meadows, wet heathland and fens with stands of its host plant, the Marsh Gentian (*Gentiana pneumonanthe*). In the Alps the Willow Gentian (*G. asclepiadea*) is used as well. The Alcon Blue has a complex life cycle and is dependent not only on the presence of its host plant but also on the presence of host ants of the genus *Myrmica*. In Southern Europe and the pre-alpine region of Germany (Nunner pers. comm.) only *M. scabrinodis* Nylander, 1846 serves as a host. In Middle and Northern Europe it is fully replaced by *M. rubra* (Linnaeus, 1758) and *M. ruginodis* Nylander, 1846 (Elmes et al. 1998). Females of *M. alcon* lay their eggs on the buds of *G. pneumonanthe*. Through basal hatching the larvae get into the flower and feed there until the fourth larval stage. After emerging from the flower head they let themselves drop on the ground and wait to be carried into

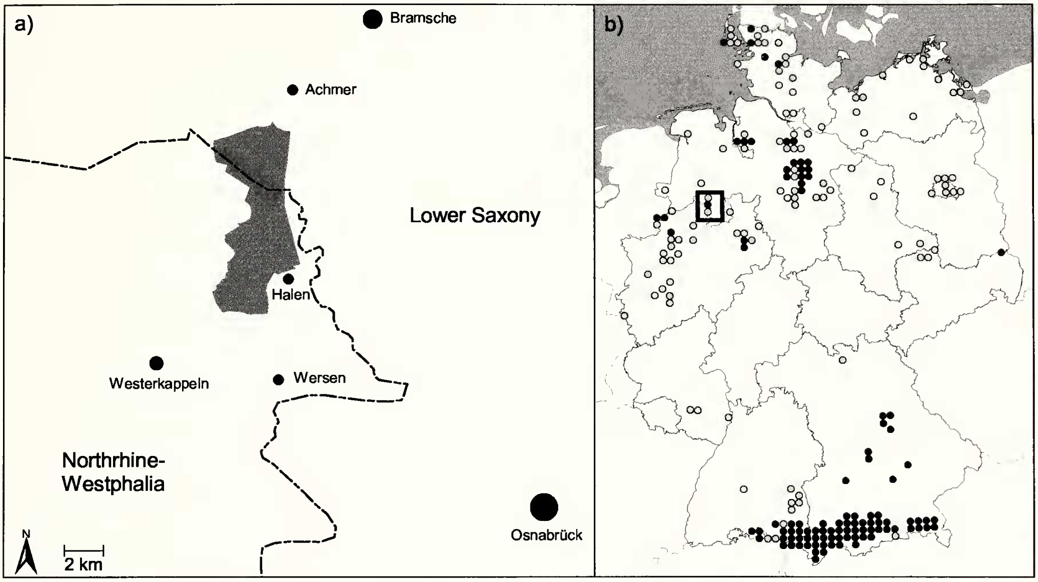


Fig. 1. Study area in Northern Germany (a) and distribution of *Maculinea alcon* in Germany (b). Grid: 10' × 6' geographic grid. Grey dots: data before 1985, black dots: data since 1985, data from: BLfU (2001), de Lattin (1957), Ebert & Rennwald (1991), Habel (2003), Harkort (1975), Kinkler & Schmitz (1971), Kolligs (2003), natural history museum Muenster (own observation), Retzlaff (1973), Retzlaff et al. (1993), Stamm (1981), Wagener & Niemeyer (2003) and M. Goldschalt, H. G. Joger, A. Krismann, A. Nunner, T. Marktanner, R. Reinhardt, T. Schulte (in each case pers. comm.).

a nest of their host ant where they live 10 to 22 months until pupation (Schönrogge et al. 2000; Thomas et al. 1998).

G. pneumonanthe (Gentianaceae) is distributed throughout Europe and Asia and has its core range in Western Europe (Korneck et al. 1998). The perennial plant flowers between July and September on oligotrophic humid sites such as litter meadows ('Streuwiesen') and moist to wet heathland (Oberdorfer 2001; Sebald et al. 1996). The light-requiring *G. pneumonanthe* grows up to 50 cm high with up to 10 shoots and up to 25 flowers per shoot (Ellenberg 1996; Rose et al. 1998). The reproduction only takes place by the means of its small seeds, which are adapted to short distance wind dispersal (Oostermeijer et al. 1998). For successful germination the seeds require moist and bare soil (Kesel & Urban 1999).

In Central Europe and in Germany *G. pneumonanthe* is declining. This is due to an intensified agricultural use on one hand. On the other hand the abandonment of smaller unprofitable habitats supports the succession on these sites. Both factors endanger the survival of the Marsh Gentian.

Study area. The study area is located in the district Steinfurt in the north of North Rhine-Westphalia adjacent to Lower Saxony (Fig. 1). The study site is part of a military training area. The vegetation is dominated by wet grasslands (*Molinietalia*) with some patches of *Agrostietalia* and *Nardo-Callunetea*. *Gentiana pneumonanthe* was growing within two sites (7,500 m^2 and 15,000 m^2) of the study area, but only on the bigger site *Maculinea alcon* was present in 2002. This place was surrounded by wood and consisted of the dominating *Juncus-Succisa pratensis* association with patches of *Ericion tetralicis*. Within this site the host plant grew on an area of about 3,200 m^2.

Tab. 1. Habitat structure parameters at occupied (n = 124) and unoccupied (n = 95) *Gentiana pneumonanthe* shoots (Mann-Whitney *U* Test: *** P <0.001, * P <0.05). *n G. pneumonanthe*: number of other shoots near the observed specimen; prominence: gentian shoot height minus average vegetation height.

Parameter	Minimum – Maximum		Median		U	P
	occupied	unoccupied	occupied	unoccupied		
Flowers per shoot	1–14	1–10	4	2	2847	***
Shoot height [cm]	22–60	22–51	39	35	3784	***
Average vegetation height [cm]	25–55	25–55	45	50	3397	***
Prominence [cm]	-29–20	-30–6	-3.4	-15	2030	***
n *Gentiana pneumonanthe*	0–13	0–11	5	4	4981	*
Horizontal herbaceous cover [%] in 30 cm	0–95	2.5–95	10	50	3751	***

Field Study. In summer 2002 after the flight period of *Maculinea alcon* all shoots of *Gentiana pneumonanthe* were checked for eggs. For each gentian shoot we determined total height, the number of flowers and the height of each flower. The eggshells were counted bud-wise distinguishing between top, middle and base of flower, calyx, leave and stalk. For microhabitat analysis the following parameters were collected within a radius of 50 cm around the shoot: distance to the next shoot, number of other shoots, the maximum and average vegetation height, the vegetation cover and horizontal vegetation cover in 10 to 45 cm height above soil surface (estimated in 5%-steps). A grid of 10 × 10 m was put on the study site to determine these parameters also on a bigger scale. For data analysis we calculated the difference of the shoot height and average vegetation height to show the 'prominence' of the host plant. Negative values express a negative prominence, which means the shoot is smaller than the surrounding vegetation. Positive values show accordingly a positive prominence of the gentian shoot.

Data Analysis. Literature data showed that a single *Maculinea alcon* female lays on the average 50–100 eggs (Maes et al. 2004). Meyer-Hozak (2000) found out that the sibling species *Maculinea rebeli* lays 100–150 eggs per female. The primary sex ratio in a population is 1 : 1 (for *M. rebeli*: Kockelke et al. 1994; Meyer-Hozak 2000). We therefore used the total egg count from this study to estimate the adult population size in 2002.

To assess the explanatory power of different variables on the occupancy of gentian shoots we used a stepwise-forward logistic regression. All statistical analysis was performed with SPSS 11.0.1 statistical analysis package.

Results

We found a total of 219 Marsh Gentian shoots with 824 flowers. Of those, 124 shoots (57%) and 473 flowers (57%) were occupied with 1,787 eggs. Based on the total egg count the adult population size was estimated at 18–36 individuals. The preferred place of oviposition was the calyx in 70% of the cases, followed by the flower with 25%. The stem and the leaves played a minor role in egg deposition (Fig. 2). The height distribution of the eggs and the flowers were quite similar. About 2/3 of both flowers and eggs were found at 26 to 40 cm above ground (Fig. 3).

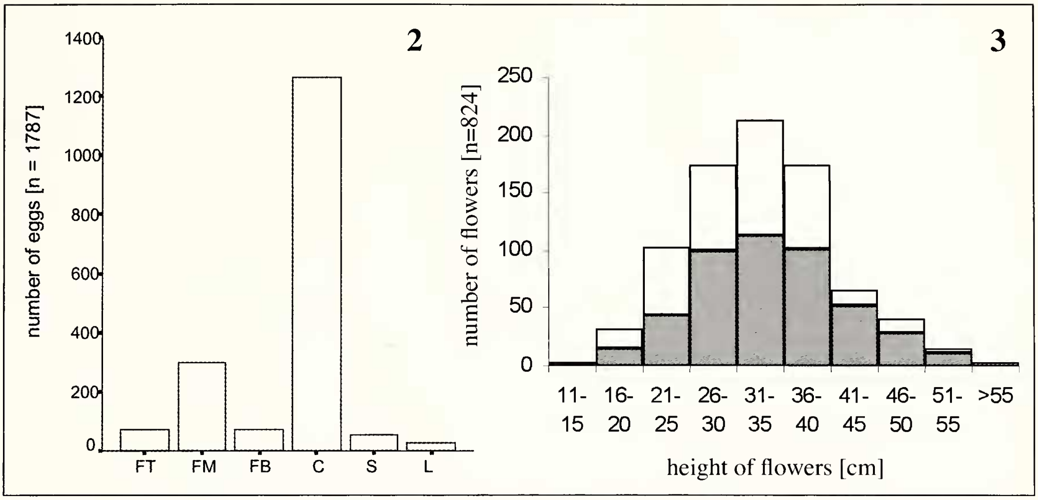


Fig. 2. Oviposition places on *Gentiana pneumonanthe* (FT = flower top, FM = flower middle, FB = flower base, C = calyx, S = stalk, L = leave).
Fig. 3. Height of occupied (grey) and unoccupied (white) flowers of *Gentiana pneumonanthe*.

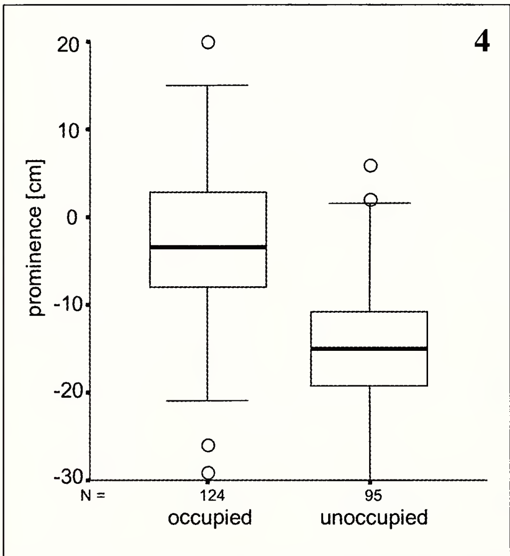
The vegetation at the egg-deposition places was relatively high and dense. Maximum vegetation height ranged from 80 to 100 cm. Vegetation cover was mostly 100%, only in some cases it was with 80–95% slightly less dense. The Marsh Gentians were scattered over the whole site but had a clustered occurrence in some places especially along old tank tracks. Most part of the study site was dominated by the Purple Moor Grass (*Molinia caerulea*) and was characterized by a vivid change of hummocks and hollows. Only some gentian shoots were found on a drier and more even area, which was dominated by the Tufted Hair-grass (*Deschampsia cespitosa*).
Occupied gentians were generally higher and had more flowers than unoccupied specimen. High average vegetation height and low horizontal vegetation cover decreased the likelihood of a host plant to be accepted for oviposition (Tab. 1). Most occupied stalks were higher or only little lower than the average vegetation (Fig. 4). The more prominent a shoot the more eggs it received (Fig. 5).
The distribution of occupied and unoccupied Marsh Gentian shoots was best explained by the combination of height difference (prominence), number of flowers per stalk and number of other Marsh Gentian shoots in the proximity. The logistic regression model classified 78% of the data correctly by means of these three parameters (Tab. 2).
The hatched grids in Fig. 6 show the average height difference. The more prominent the gentian shoots were the more likely they were to be chosen for oviposition.

Discussion

Microclimatic aspects play an important role in butterfly oviposition (Fartmann 2004; Porter 1992; Thomas et al. 1998). As all gentians grew in sunny areas they were theoretically equally available for egg deposition. However, only about half of the shoots were occupied with eggs. Not only the size of the plant and the number of flowers,

Tab. 2. Stepwise-forward logistic regression model on the influence of habitat structure parameters on the egg deposition preference of *Maculinea alcon* (host plant shoots n = 219). n.s. = not significant; n *Gentiana pneumonanthe*: number of other shoots near the observed specimen; prominence: gentian shoot height minus average vegetation height.

Parameter	Coefficient B	SD	P	R	Model improvement Chi²
Constant	-0.027	0.497	n.s.	.	.
Prominence [cm]	0.143	0.025	<0.001	0.326	76.49
Flowers per shoot	0.263	0.089	<0.005	0.150	10.83
n *Gentiana pneumonanthe*	0.139	0.052	<0.05	0.132	7.78
Shoot height [cm]	0.657	-	n.s.	0.000	.
Average vegetation height [cm]	0.657	-	n.s.	0.000	.
Horizontal herb cover [%]	0.159	-	n.s.	0.000	.
Model summary	$Chi^2 = 95.1$, df = 3, P <0.001				
Correctly classified	78.1%				



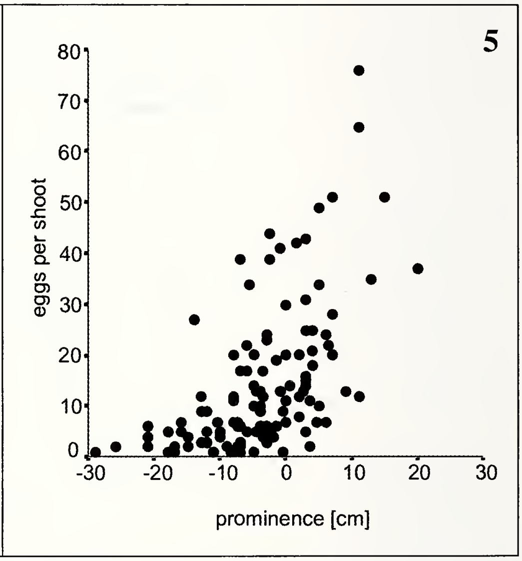


Fig. 4. Difference of hostplant height and average vegetation height (prominence) of occupied and unoccupied *Gentiana pneumonanthe* shoots (Mann-Whitney *U* Test: U = 2030, P <0.001). Compare Tab. 1 for statistics.

Fig. 5. Number of eggs per *Gentiana pneumonanthe* shoot in relation to the prominence (host plant shoots n = 124). $r_s = 0.622$, n = 124, P <0.01. Prominence: gentian shoot height minus average vegetation height.

but especially the shoot height relative to the height of the surrounding vegetation are important. Results of the logistic regression model show that the preferred oviposition places are shoots with many flowers that protrude the vegetation and are surrounded by other *Gentiana* shoots.

It is a common phenomenon that females choose large and conspicuous host plant individuals (Porter 1992). *Maculinea rebeli* prefers luxuriant specimens of its host plant *Gentiana cruciata* that are easy to reach (Dolek et al. 1998; Meyer-Hozak 2000). First, visual attraction is an important factor when searching for a suitable host plant

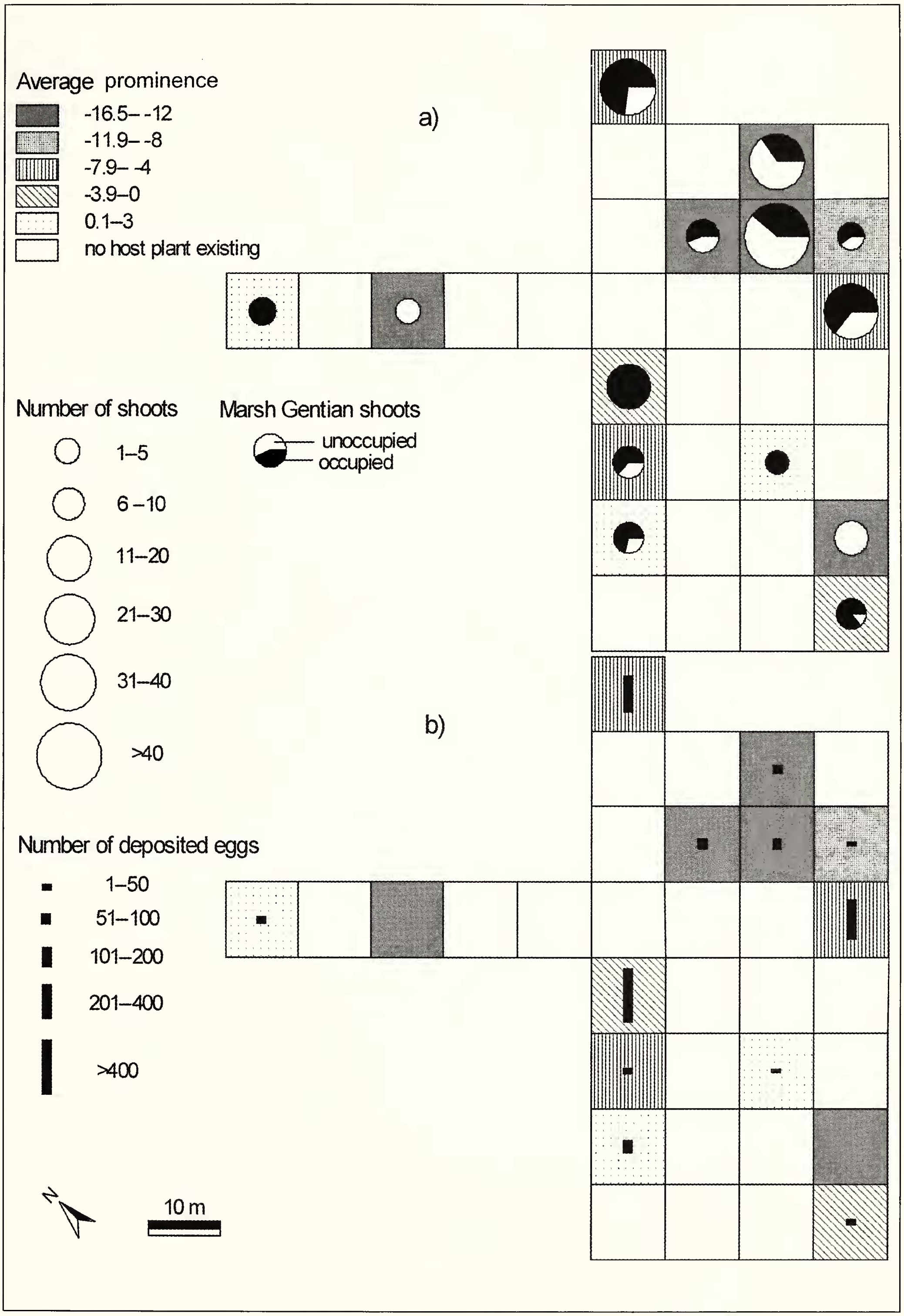


Fig. 6. Occupied and unoccupied Marsh Gentian shoots (a) and number of deposited eggs (b) per grid in relation to promincence. The average prominence is the median of all recorded height differences per grid.

(Dolek et al. 1998). Prominent shoots can be seen easily and are hence predestined as oviposition site. Second, shoots that grow higher than their surrounding vegetation are less shaded and offer better microclimatic conditions for a quick development of eggs and larvae. Besides it is risky to lay eggs on gentians hidden in dense vegetation because of the orb-web spiders, which are common in unmown meadows in this time of the year (Nunner pers. comm.). Third, bigger gentians may produce bigger buds and therefore offer more food resources for the larvae.

Over occupation of the shoots is seldom. Only 10 out of 124 shoots had more than 6 eggs per flower. About 4 to 6 *Maculinea alcon* larvae can feed on one flower (Elmes & Thomas 1987; Ebert & Rennwald 1991), which means that for almost all larvae there are sufficient food resources.

Despite the impression that the striking white eggs of *M. alcon* are mainly laid on the blue flowers of *Gentiana pneumonanthe*, we found almost three quarters of the eggs on the calyx but only one quarter on the flower. On the foothills of the Alps, Krismann (2000) found a similar distribution pattern on both *G. pneumonanthe* and *G. asclepiadea*. This oviposition pattern makes sense taking into account that the larvae of *M. alcon* leave the eggs through basal hatching (Thomas et al. 1991). They bore through the calyx and directly move to their food resource, the plant ovary.

Since *M. alcon* larvae hatch rapidly, the strong exposition of the eggs might be contributing to a fast larval development (Porter 1992). Within 3–4 weeks the larvae have to reach the fourth larval instar and need therefore optimal microclimatic conditions such as on the concealed flowers are provided. Although the eggs are more or less unprotected and very conspicuous, they are rarely parasitised. This may be due to the thick eggshells, which effectively prevent perforation by parasitoid wasps (Thomas et al. 1991). Thick eggshells may further protect against bad or hot weather.

The study site lies fallow; there is no regular utilization or care. Therefore it is dominated by the Purple Moor Grass (*Molinia caerulea*). Vegetation cover was mostly 100%. Nevertheless the Marsh Gentian is able to survive in such dense vegetation because of its longevity (Rose et al. 1998). On the study site mostly adult *G. pneumonanthe* grow. Oostermeijer et al. (1994) call this population type 'senile'. However, a senile population provides advantage for *M. alcon* regarding the suitability of egg deposition as most of the plants are relatively high and mostly covered with several flowers. This is reflected in the proportion of occupied gentians, which was with over 50% very high (compare Habel 2003; Krismann 2000). Still for a long-term survival of the gentian population and also of the Alcon Blue population a rejuvenation of the host plants is necessary which means creating gaps of bare soil.

There are different ways to assure the regeneration of *G. pneumonanthe* populations. Kesel & Urban (2000) and WallisDeVries (2004) suggest that small-scale sod cutting is best to promote existing gentian populations. Gaps are created in which the seeds can germinate and the young seedlings can grow protected. Though mowing is probably the better alternative to prevent from floristic impoverishment, to keep the vegetation open and to support the growth of accessible gentian shoots (Nunner pers. comm.). The best time is in October when the gentian seeds are mature and the *M. alcon* larvae are adopted (Briemle & Ellenberg 1994; Nunner pers. comm.). The hay should be taken away to prevent litter accumulation (Fartmann & Mattes 1997). Trautner et al. (2004) and WallisDeVries (2004) suggest that extensive grazing is also appropriate as management for *M. alcon* habitats with *G. pneumonanthe* as host plant. The gentian plants grow less luxurious but the small flowers seem to offer enough food for the *Maculinea* larvae until adoption. However, grazing is not an alternative when *G. pneumonanthe* sites are small because of the risk of local overgrazing or when *G. asclepiadea* is the host plant because it is more sensitive to browsing.

As most Marsh Gentian plants on the study site grow along old tank tracks it may be supposed that occasional mechanic disturbance through tanks or other means can have positive effects if it happens only every couple of years.

Acknowledgements

The idea for this study came from C. Artmeyer. H. Mattes gave expert advice about the manuscript. We thank N. Anthes, K. Arnold, G. Hermann, A. Nunner and M. WallisDeVries for valuable comments. Distribution data of *Maculinea alcon* were provided by H. Dudler, M. Goldschalt, H. G. Joger, A. Krismann, T. Marktanner, A. Nunner, R. Reinhardt and H. Retzlaff.

References

Als, T. D., D. R. Nash & J. J. Boomsma 2001. Adoption of parasitic *Maculinea alcon* caterpillars (Lepidoptera: Lycaenidae) by three *Myrmica* ant species. – Animal Behaviour **62**: 99–106.

Als, T. D., R. Vila, N. P. Kandul, D. R. Nash, S.-H. Yen, Y.-F. Hsu, A. A. Mignault, J. J. Boomsma & N. E. Pierce 2004. The evolution of alternative parasitic life histories in large blue butterflies. – Nature **432**: 386–390.

Anthes, N., T. Fartmann, G. Hermann & G. Kaule 2003. Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine *Euphydryas aurinia* colonies. – Journal of Insect Conservation **7**: 175–185.

Bayerisches Landesamt für Umweltschutz (BLfU) 2001. Artenschutzkartierung Bayern: Arbeitsatlas Tagfalter – Augsburg.

Briemle, G. & H. Ellenberg 1994. Zur Mahdverträglichkeit von Grünlandpflanzen. – Natur und Landschaft **69**: 139–147.

de Lattin, G. 1957. Die Lepidopteren-Fauna der Pfalz. I. Teil. – Mitteilungen der Pollichia (ser. 4) **3**: 51–167.

Dennis R. L. H. & H. T. Eales 1997. Patch occupancy in *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. – Journal of Insect Conservation **1**: 167–176.

Dolek, M., A. Geyer & R. Bolz 1998. Distribution of *Maculinea rebeli* and hostplant use on sites along the river Danube. – Journal of Insect Conservation **2**: 85–89.

Dudler, H., H. Kinkler, R. Lechner, H. Retzlaff, W. Schmitz & H. Schumacher 1999. Rote Liste der gefährdeten Schmetterlinge (Lepidoptera) in Nordrhein-Westfalen. Pp. 575–626. – *In*: Landesanstalt für Ökologie, Bodenordnung und Forsten/Landesamt für Agrarordnung Nordrhein-Westfalen (LÖBF), Rote Liste der gefährdeten Pflanzen und Tiere in Nordrhein-Westfalen, 3. Fassung – LÖBF-Schriftenreihe 17, Recklinghausen.

Ebert, G. & E. Rennwald 1991. Die Schmetterlinge Baden-Württembergs **2** (2). – Ulmer, Stuttgart. 535 pp.

Elfferich, N. W. 1988. Zuchterfahrungen mit *Maculinea alcon* (Denis & Schiffermüller, 1775) (Lepidoptera, Lycaenidae). – Mitteilungen der Entomologischen Gesellschaft Basel **38**: 134–150.

Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. – Ulmer, Stuttgart. 1059 pp.

Elmes, G. W. & J. A. Thomas 1987. Die Gattung *Maculinea*. Pp. 354–368. – *In*: Lepidopterologen-Arbeitsgruppe, Tagfalter und ihre Lebensräume. – Schweizerischer Bund für Naturschutz, Basel.

Elmes, G. W., J. A. Thomas, O. Hammarstedt, M. L. Munguira, J. Martin & J. Van Der Made 1994. Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly *Maculinea alcon* (Denis et. Schiff.) (Lepidoptera). – Memorabilia Zoologica **48**: 55–68.

Elmes, G. W., J. A. Thomas, J. C. Wardlaw, M. E. Hochberg, R. T. Clarke & D. J. Simcox 1998. The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies. – Journal of Insect Conservation **2**: 67–78.

Fartmann, T. 2004. Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales – Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. – Abhandlungen aus dem Westfälischen Museum für Naturkunde **66** (1): 1–256.

Fartmann, T. & H. Mattes 1997: Heuschreckenfauna und Grünland – Bewirtschaftungsmaßnahmen und Biotopmanagement. Pp. 179–188. – *In*: H. Mattes (ed.), Ökologische Untersuchungen zur Heuschreckenfauna in Brandenburg und Westfalen. – Arbeiten aus dem Institut für Landschaftsökologie Münster **3**.

Habel, J. C. 2003. Auswirkungen der Fragmentierung von Lebensräumen am Beispiel von *Maculinea alcon* (Denis & Schiffermüller 1775). – Diplomarbeit, Institut für Ökologie und Umweltchemie, Universität Lüneburg. 83 pp.

Harkort, W. 1975. Schmetterlinge in Westfalen (ohne Ostwestfalen). Fundortkarten und Fundortlisten (Stand: Ende 1974). – Dortmunder Beiträge zur Landeskunde: Naturwissenschaftliche Mitteilungen **9**: 33–102.

Hochberg, E., J. A. Thomas & G. W. Elmes 1992. A modelling study of the population dynamics of a Large Blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. – Journal of Animal Ecology **61**: 397–409.

Kesel, R. & K. Urban 1999. Population dynamics of *Gentiana pneumonanthe* and *Rhynchospora fusca* during wet heathland restoration. – Applied Vegetation Science **2**: 149–156.

Kesel, R. & K. Urban 2000. Species dynamics in wet heathland restoration. – Proceedings IAVS Symposium: 286–290.

Kinkler, H. & W. Schmitz 1971. Die Tagfalter des Bergischen Landes. – Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal **24**: 20–63.

Kockelke, K., G. Hermann, G. Kaule, M. Verhaagh & J. Settele 1994. Zur Autökologie und Verbreitung des Kreuzenzian-Ameisenbläulings, *Maculinea rebeli* (Hirschke, 1904). – Carolinea **52**: 93–109.

Kolligs, D. 2003. Schmetterlinge Schleswig-Holsteins. – Wachholtz, Kiel. 212 pp.

Korneck, D., M. Schnittler, F. Klingenstein, G. Ludwig, M. Takla, U. Bohn & R. May 1998. Warum verarmt unsere Flora? Auswertung der Roten Liste der Farn- und Blütenpflanzen Deutschlands. Pp. 299–444. – *In*: Bundesamt für Naturschutz (eds.), Ursachen des Artenrückgangs von Wildpflanzen und Möglichkeiten zur Erhaltung der Artenvielfalt. – Schriftenreihe für Vegetationskunde **29**, Bonn Bad Godesberg.

Krismann, A. 2000. Zum Eiablageverhalten von *Maculinea alcon* (D. & S., 1775) an *Gentiana pneumonanthe* und *Gentiana asclepiadea*. Pp. 103–110. – *In*: J. Settele & S. Kleinewiedtfeld (eds.), Populationsökologische Studien an Tagfaltern **2**. UFZ-Bericht. – UFZ Leipzig-Halle, Leipzig.

Liebig, W.-H. 1989. Bemerkungen zur Biologie von *Maculinea alcon* Schiff. (Lep., Lycaenidae). – Entomologische Nachrichten und Berichte **33**: 117–121.

Maes, D., W. Vanreusel, W. Talloen & H. van Dyck 2004. Functional conservation units for the endangered Alcon Blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). – Biological Conservation **120**: 229–241.

Marktanner, T. 1985. Die Bedeutung des Schwalbenwurzenzians als Futterpflanze von *Maculinea alcon* (Lep.: Lycaenidae) im oberschwäbischen Alpenvorland und die Verbreitung der Lycaenide in diesem Raum. – Entomologische Zeitschrift **95**: 257–272.

Meyer-Hozak, C. 2000. Population biology of *Maculinea rebeli* (Lepidoptera: Lycaenidae) on the chalk grasslands of Eastern Westphalia (Germany) and implications for conservation. – Journal of Insect Conservation **4**: 63–72.

Munguira, M. L. & J. Martin 1999. Action plan for the *Maculinea* Butterflies in Europe. – Nature and Environment **97**. Council of Europe Publishing, Strasbourg. 63 pp.

Oberdorfer, E. 2001. Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete. – Ulmer, Stuttgart. 1051 pp.

Oostermeijer, J. G. B., R. V. T. Veer & J. C. M. Den Nijs 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. – Journal of Applied Ecology **31**: 428–438.

Oostermeijer, J. G. B., S. H. Luijten, Z. Krenová & H. C. M. Den Nijs 1998. Relationships between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. – Conservation Biology **12**: 1042–1053.

Porter, K. 1992. Eggs and egg-laying. Pp. 46–72. – *In*: Dennis, R. L. H. (ed.), The ecology of butterflies in Britain. – Oxford University Press, Oxford.

Pretscher, P. 1998. Rote Liste der Großschmetterlinge (Macrolepidoptera). – Schriftenreihe Landschaftspflege und Naturschutz **55**: 87–111.

Retzlaff, H. 1973. Die Schmetterlinge von Ostwestfalen-Lippe und einigen angrenzenden Gebieten Hessens und Niedersachsens (Weserbergland, südöstliches Westfälisches Tiefland und östliche Westfälische Bucht). I. Teil. – Berichte des Naturwissenschaftlichen Vereins Bielefeld **21**: 129–248.

Retzlaff, H., H. Dudler, C. Finke, R. Pähler, K. Schnell & W. Schulze 1993. Zur Schmetterlingsfauna von Westfalen. Ergänzungen, Neu- und Wiederfunde. – Mitteilungen der Arbeitsgemeinschaft ostwestfälisch-lippischer Entomologen **9** (2): 37–66.

Rose, R. J., R. T. Clarke & S. B. Chapman 1998. Individual variation and the effects of weather, age and flowering history on survival and flowering of the long-lived perennial *Gentiana pneumonanthe*. – Ecography **21**: 317–327.

Sebald, O., S. Seybold, G. Philippi & A. Wörz (eds.) 1996. Die Farn- und Blütenpflanzen Baden-Württembergs, vol. **5**: Spezieller Teil (Spermatophyta, Unterklasse Asteridae) Buddlejaceae bis Caprifoliaceae. – Ulmer, Stuttgart. 539 pp.

Schönrogge, K., J. C. Wardlaw, J. A. Thomas & G. W. Elmes 2000. Polymormphic growth rates in myrmecophilous insects. – Proceedings of the Royal Society of London B **267**: 771–777.

Stamm, K. 1981. Prodomus der Lepidopteren-Fauna der Rheinlande und Westfalens. – Solingen.

Thomas, J. A., M. L. Munguira, J. Martin & G. W. Elmes 1991. Basal hatching by *Maculinea* butterfly eggs: a consequence of advanced myrmecophily. – Biological Journal of the Linnean Society **44**: 175–184.

Thomas, J. A., D. J. Simcox, J. C. Wardlaw, G. W. Elmes, M. E. Hochberg & R. T. Clarke 1998. Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. – Journal of Insect Conservation **2**: 39–46.

Thomas J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis & B. Goodger 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. – Proceedings of the Royal Society of London B **268**: 1791–1796.

Trautner, J., G. Hermann & J. Rietze 2004. Weidewirkungen auf Tierarten und Zönosen. Pp. 275–285. – *In*: D. Lerderbogen, G. Rosenthal, D. Scholle, J. Trautner, B. Zimmermann & G. Kaule (eds.), Allmendweiden in Südbayern: Naturschutz durch landwirtschaftliche Nutzung. – Angewandte Landschaftsökologie Heft **62**. Bundesamt für Naturschutz (BfN), Bonn.

van Dyck, H., J. G. B. Oostermeijer, W. Talloen, V. Feenstra, A. van der Hidde & I. Wynhoff (2000). Does the presence of ants matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? – Proceedings of the Royal Society of London B **267**: 861–866.

van Swaay, C. A. M. & M. Warren 1999. Red data book of European butterflies (Rhopalocera). – Nature and Environment **99**. Council of Europe Publishing, Strasbourg. 260 pp.

Wagener, S. & B. Niemeyer 2003. Beitrag zur Großschmetterlingsfauna des Kreises Borken. – Abhandlungen aus dem Westfälischen Museum für Naturkunde **65** (1/2): 149–201.

WallisDeVries, M. F. 2004. A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. – Conservation Biology **18**: 489–499.

Wynhoff, I. 1998. The recent distribution of the *Maculinea* species. – Journal of Insect Conservation **2**: 15–27.

Wynhoff, I., C. A. M. Van Swaay & J. Van Der Made 1999. Veldgids Dagvlinders. – Stichting Uitgeverij KNNV, Utrecht. 224 pp.